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Energetic consequences of time-activity budgets for a breeding seabird

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Abstract

How animals allocate their time to different behaviours has important consequences for their overall energy budget and reflects how they function in their environment. This potentially affects their ability to successfully reproduce, thereby impacting their fitness. We used accelerometers to record time-activity budgets of 21 incubating and chick-rearing kittiwakes (*Rissa tridactyla*) on Puffin Island, UK. These budgets were examined on a per day and per foraging trip basis. We applied activity-specific estimates of energy expenditure to the kittiwakes' time-activity budgets in order to identify the costs of variation in their allocation of time to different behaviours. Estimates of daily energy expenditure for incubating kittiwakes averaged 494 $\pm$ 20 kJ d^{-1} while chick-rearing birds averaged 559 $\pm$ 11 kJ d^{-1}. Time-activity budgets highlighted that kittiwakes did not spend a large proportion of their time flying during longer foraging trips, or during any given 24-h period. With time spent flying highlighted as the driving factor behind elevated energy budgets, this suggests behavioural compensation resulting in a possible energetic ceiling to their activities. We also identified that kittiwakes were highly variable in the proportion of time they spent either flying or on the water during foraging trips. Such variation meant that using forage trip duration alone to predict energy expenditure gave a mean error of 19% when compared to estimates incorporating the proportion of a foraging trip spent flying. We have therefore highlighted that trip duration alone is not an accurate indicator of energy expenditure.

Introduction

During their breeding periods, many animals must increase their foraging effort in an attempt to provide enough food not only for their own survival but also for the survival and growth of their offspring (Grémillet, 1997). As movement accounts for a large proportion of energy expenditure in many free-ranging animals (Brit-Friesen *et al.*, 1989), this elevated foraging effort impacts the energy budgets of individuals. Thus, how animals allocate their time to different behaviours during the breeding period can be a key component to their eventual reproductive success and fitness (Gittleman & Thompson, 1988).

Understanding the interactions between behaviour, energetics and fitness is a key consideration for comprehending the roles of organisms in their ecosystems (Tomlinson *et al.*, 2014). However, free-ranging animals are often difficult to observe over long periods of time without interruption. Seabirds exemplify this difficulty, with individuals often foraging far out at sea, where directly observing their behaviour is highly impractical. Conventionally, presence or absence of individuals at their nest has been used to indicate how they allocate their time during the breeding season (Granadeiro *et al.*, 1998; Lewis *et al.*, 2001), yet this approach lacks detailed information regarding activity when away from the nest. As time away from the nest comprises of a variable combination of time spent in either active behaviours (such as flight or foraging) or resting, allocation of time to activity within this period is likely to be of major energetic importance. Using animal-borne data loggers such as accelerometers, which measure an animal's body acceleration continuously, it is now possible to collect continuous measurements of the behaviour of individuals to generate detailed time-activity budgets regardless of location (e.g. Shepard *et al.*, 2008; Halsey *et al.*, 2009b).

While the biological implications of variation in time-activity budgets are informative alone, it is even more informative to estimate how differences in time allocation to behaviour relate to energy expenditure. Currently, the most prominent approaches for estimating energy expenditure *in situ* are the doubly labelled water (DLW) method and the heart rate method. Although these techniques have greatly enhanced our understanding of energy expenditure in wild animals, they do have limitations, notably the DLW method has poor temporal

resolution (Butler *et al.*, 2004; Shaffer, 2011) and the heart rate method generally requires surgical implantation of a data logger (Butler *et al.*, 2004). Alternatively, by combining time-activity budgets with either laboratory- or model-derived estimates of activity-specific energy expenditure, time-energy budgets can be constructed (Goldstein, 1988). Such an approach is not novel in principle, yet the inclusion of accelerometry-derived time-activity budgets now allows for this approach to be applied to continuous, high-resolution behavioural information from highly mobile animals (Shamoun-Baranes *et al.*, 2012). This alternative approach then allows estimation of energy expenditure of free-ranging animals at a finer temporal scale than the DLW method, and in a less invasive manner than the heart rate method.

In this study, we combine accelerometer-derived time-activity budgets with published values of activity-specific metabolic costs to estimate the energy expenditure of free-ranging black-legged kittiwakes *Rissa tridactyla*. Kittiwakes are a suitable species on which to apply this approach as they have a relatively simple repertoire of coarse-scale behaviours, consisting of flight, being on water, and attending the nest; these behaviours are readily identifiable from accelerometry traces (Collins *et al.*, 2015). To date, energy expenditure of kittiwakes has been estimated numerous times with the DLW method (Gabrielsen, Mehlum & Nagy, 1987; Thomson, Furness & Monaghan, 1998; Golet, Irons & Costa, 2000; Jodice *et al.*, 2002, 2003; Welcker *et al.*, 2009, 2014; Schultner *et al.*, 2010), highlighting variation within and between individuals and populations, as well as showing that time away from the colony is an important component of total daily energy expenditure (DEE) (Fyhn *et al.*, 2001). Furthermore, in a study by Welcker *et al.* (2010) which employed the DLW method, kittiwakes exhibited remarkably similar DEE across years with different prey availability. They therefore posited that kittiwakes were operating at an intrinsic energy ceiling, whereby individuals apparently had a limit to the amount of energy they expend (Drent & Daan, 1980). It is likely that kittiwakes exhibit behavioural compensation, whereby they adjust time spent in more energetically demanding activities to limit energy expenditure (Elliott *et al.*, 2014a), however, the poor temporal resolution of the DLW method coupled with a lack of continuous behavioural data has largely inhibited the possibility of identifying evidence for this. In this study, by deploying accelerometers on both incubating and chick-rearing kittiwakes, we quantify how kittiwakes allocate their time, and what the energetic consequences of variation in time allocation are. By linking behaviour to energy expenditure, we set out to identify if there is evidence for behavioural compensation.

Materials and methods

Data collection

Tri-axial accelerometers (X8 m-3 Gulf Coast Data Concepts, LLC; recording range ±8 g, resolution: 0.001 g, weight: 14 g), set to record at 25 Hz, were deployed on 50 kittiwakes over three breeding seasons. Accelerometers were attached to feathers on the centre of the backs of individuals using clothed black Tesa® tape. The placement of the accelerometer was kept as consistent as possible across all birds. Mean body mass was 365 ± 31 g (mean ± SD), ranging from 310 to 435 g, with data loggers weighing on average 3.8 ± 0.3% of body mass. Twenty-eight accelerometers were retrieved, of which 21 were functioning correctly. Of these 21 accelerometers, 17 were from individuals during the early chick-rearing stage (chicks less than 10 days old), and four were from adults at the late incubation stage. Accelerometers were deployed on birds at a similar point within the incubation or chick-rearing process as energy expenditure changes dependent on time in these stages (Fyhn *et al.*, 2001). Accelerometers that were not retrieved were either deployed on individuals who evaded recapture, or had fallen off before retrieval was attempted. Accelerometers not removed would have fallen off within 2 weeks. Deployment time for recaptured birds averaged 58 ± 22 h and ranged from 23 to 114 h, during which time birds exhibited apparently normal breeding behaviour, including nest attendance (comprising of care of eggs or chicks) or absence from the nest (most likely on foraging trips). Fieldwork was carried out on Puffin Island, North Wales in July 2012, July 2013 and July 2014. All work was carried out under Countryside Council for Wales permit numbers (37727: OTH:SB:2012, 44043:OTH:SB:2013, 53628:OTH:SB:2014).

Behavioural assignments

To generate time-activity budgets, acceleration data were assigned to three coarse-scale behaviours: 'nest attendance', 'on water' and 'flying'. Although finer scale behaviours such as foraging, preening and courtship are exhibited by kittiwakes, the amount of time these behaviours take up is relatively little (Jodice *et al.*, 2003). As per Collins *et al.* (2015), behaviours were assigned using a simple method that categorizes different activity types based on readily calculable metrics indicating body orientation or amount of movement. This method has been shown to give high accuracy (>95%) of coarse-scale behaviour assignments in kittiwakes (Collins *et al.*, 2015). Behaviours of 'nest attendance' and 'on water' were assigned depending on the body angle of the bird; periods when the bird was at a lower angle were assigned as 'on water', and periods at which the bird was at a higher body angle were identified as being 'on land'. The body angle thresholds at which these behaviours were separated were specific to each individual. When classified as on land, based on observations of their behaviours, the birds were assumed to be attending their nest, and were thus assigned the behaviour 'nest attendance'. Flight was assigned based on the standard deviation of acceleration values in the heave axis, with higher values indicating movement in this channel relating to flight. Flight was not separated into flapping or gliding, although inspection of acceleration traces suggested that the kittiwakes flapped much more than glide.

Time-activity budgets

We constructed time-activity budgets at two scales of interest; daily and complete foraging trips. For each day and each

foraging trip, we determined the amount and proportion of time spent on the three coarse-scale behaviours. For daily time-activity budgets, only records consisting of 24 h of continuous data starting at midnight were used. The sample size for incubating birds was 3 days' worth of data from three individuals, and that for chick-rearing birds was 25 days' worth of data from 17 individuals. Foraging trips were defined as a period in which the bird flew from the land, spent time on water, and then returned to the land, with trips varying in duration. Only trips over 30 min were used, to exclude periods when birds might have left the land for reasons other than foraging (such as researcher disturbance or predator avoidance (Collins *et al.*, 2014)). In total, 146 trips were identified and analysed. Trips were further separated into two types; those which started 1 day and finished the next were assigned as overnight trips ($n = 18$), while those starting and finishing on the same day were assigned as day trips ($n = 128$).

Time-energy budgets

To estimate the energy expenditure for the behaviours 'nest attendance' and 'on water', we used the intraspecific allometric equations for resting metabolic rates of these behaviours reported in Humphreys, Wanless & Bryant (2007). For estimating the energy cost of flight, we used the modelling software Flight 1.25 (http://www.bristol.ac.uk/biology/people/colin-j-pennycuick/index.html, Pennycuick (2008)). We used the default values for a kittiwake wingspan (0.947 m) and aspect ratio (9.44 m^2) and input mass per bird from our data. We included a payload of 14 g to account for the accelerometer and set altitude at 10 m above sea level. Standard errors of energy cost estimates were calculated through 10 000 iterations of bootstrapping with replacement from the distribution of the activity-specific energy costs ($n = 21$).

To estimate the most accurate total DEE possible for each bird, we input individual kittiwake mass into our equations for activity-specific energy expenditure and combined these activity-specific costs with each individual's time-activity budget. These values are used to report estimates of DEE for the population for the incubation and chick-rearing periods overall. To get an estimate of DEE which indicates how time spent in each behaviour alone influences energy expenditure, we estimated activity-specific energy costs based on the mean kittiwake mass of 365 g and combined these with each individual's time-activity budget. This method was also used to estimate foraging trip energy expenditure. For estimates using mean mass, energy expenditure while attending the nest was calculated to be 13.6 ± 1.2 kJ h^{-1}, energy expenditure while on water was 18.8 ± 3.0 kJ h^{-1} and energy expenditure for flying was 48.24 ± 5 kJ h^{-1}. Estimating energy expenditure for these behaviours based on mean mass is justified as preliminary analysis showed no relationship between body mass and time-activity budgets.

Statistical analysis

A Welch's t-test (used due to unequal variances) was applied to test for differences in DEE between the three study years. As DEE did not significantly differ between years ($t_{13.191} = -0.494$, $P = 0.6297$), we pooled all data for analysis. A Welch's t-test was also used to test for differences in DEE between incubating and chick-rearing birds. To analyse differences in foraging trip durations and proportion of trips spent in flight between breeding stages and trip type, generalized linear mixed models (GLMMs) including these variables and the interaction between them were constructed. A GLMM was also constructed to analyse the effect of forage trip duration on the proportion of trip spent in flight. Due to each kittiwake undertaking numerous foraging trips, in all GLMMs, individual bird identity was assigned as a random factor. Models with foraging trip duration as the response variable were constructed using a Gaussian family with a log link due to the response variable conforming to assumptions of normality, while models with proportion of trip spent in flight as the response variable used a binomial family with logit link, as this response variable did not conform to assumptions of normality. To assess the accuracy of using foraging trip duration alone to predict energy expenditure, the difference between estimated energy expenditure for each foraging trip to that predicted by a general linear model between forage trip duration and energy expenditure was calculated.

P-values below 0.05 were deemed to be significant, although our analysis places a greater emphasis on graphical representation of the data due to the imprecise nature of *P*-values (Halsey *et al.*, 2015) and low sample sizes in some aspects of the study. All means are presented ± 1 standard error unless otherwise stated. All data analysis was conducted in R statistical software version R 3.2.1 (R Core Team, 2015) using 'glmmPQL' from the 'MASS' package.

Results

Time-activity budgets

Over a 24-h period, incubating and chick-rearing kittiwakes differed in how they allocated their time to the three behaviours (Fig. 1). Incubating kittiwakes spent a similar percentage of their time attending their nest as they spent on water (41.7 ± 18.4 and $43.8 \pm 20.3\%$ respectively), and proportionally less of their time in flight ($14.5 \pm 3.3\%$). Chick-rearing kittiwakes spent more of their time attending their nest ($58.9 \pm 2.4\%$), with time spent on water taking up the least amount of their daily time budget ($13.5 \pm 5.8\%$). Chick-rearing kittiwakes spent almost twice as much of their day in flight than incubating kittiwakes did ($27.6 \pm 2.1\%$).

Time spent on foraging trips, and the proportion of time spent either flying or on water within these trips, varied considerably both within and between birds. Duration of foraging trips was highly variable for all kittiwakes (Fig. 2a); mean duration of foraging trips for incubating kittiwakes was 3.10 ± 0.73 h, ranging from 0.53–9.22 h ($n = 17$), while the mean foraging trip duration for chick-rearing kittiwakes was 2.70 ± 0.20 h, ranging from 0.50–10.83 h ($n = 129$). These differences were not significant, however ($t_{19} = 1.14$, $P = 0.267$). Trip duration was significantly longer for overnight trips compared to trips starting and ending on the same

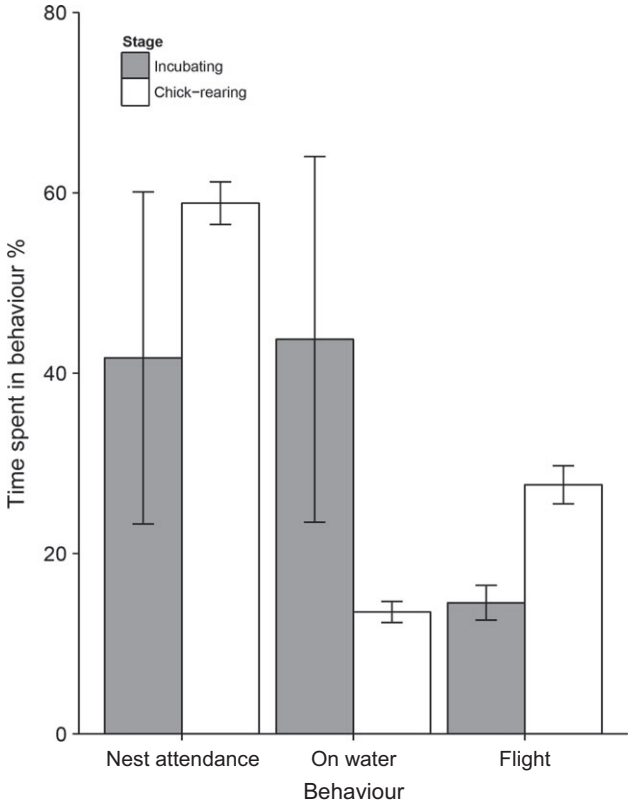

Figure 1 Mean ± SE daily percentage of time spent undertaking three recorded coarse-scale behaviours for incubating ($n = 3$) and chick-rearing kittiwakes ($n = 25$). Only days with 24 h-worth of data were used.

day (Fig. 2b) ($t_{19} = 13.48$, $P < 0.001$), with daytrips averaging 2.07 ± 0.15 h (range 0.50–7.88 h, $n = 128$) and overnight trips averaging 7.60 ± 0.47 h (range 3.67–10.83 h, $n = 18$). There was no significant interaction between breeding stage and trip type in relation to trip duration ($t_{123} = -0.60$ $P = 0.552$).

The proportion of time spent flying during each trip also varied considerably between trips (Fig. 2c and d). For incubating kittiwakes, the mean proportion of foraging trips spent flying was 53 ± 9% (ranging from 24–99%, $n = 17$) while for chick-rearing kittiwakes, the mean was 69 ± 2% (ranging from 47–99%, $n = 129$). As with foraging trip duration, percentage of foraging trip spent flying did not differ significantly between breeding stages ($t_{19} = -1.55$, $P = 0.137$). Trip type (day trip or overnight trip) had a significant effect on the proportion of time spent flying over the foraging trip, with the proportion of time spent flying during daytrips (mean = 72 ± 2%, ranging from 2–99%, $n = 128$) being significantly greater ($t_{123} = -6.78$ $P < 0.001$), than proportion of time spent flying during overnight trips (mean = 31 ± 4%, ranging from 30–74%, $n = 18$). There was no significant interaction between breeding stage and trip type in relation to proportion of time spent flying ($t_{123} = -0.35$ $P = 0.725$).

Energy expenditure

Estimated individual DEE averaged 552 ± 12 kJ d^{-1} ($n = 28$). The average for incubating kittiwakes was 494 ± 20 kJ d^{-1} ($n = 3$), which was 13% lower than chick-rearing kittiwakes which averaged 559 ± 11 kJ d^{-1} ($n = 25$), however, these estimates did not differ significantly ($t_5 = 2.0$, $P = 0.10$). Individual DEE values (range 358 ± 31–745 ± 67 kJ d^{-1}) as well as mass and time spent in each behaviour are presented in Appendix S1.

Using estimates of energy expenditure based on average mass, due to the higher energy cost per unit time of flight, kittiwakes that spent a greater proportion of the day flying had higher DEE (Fig. 3). As a result, high variation in the proportion of time individuals spent flying across the day drove the variability in estimated DEE (Fig. 3).

As foraging trips were highly variable in both duration and allocation of time to either flying or resting on water, the estimated energy expenditure across those trips also varied widely, from 14 ± 1 kJ to 368 ± 19 kJ, averaging 103.1 ± 7 kJ ($n = 153$) (Fig. 4). Expressed as rate of energy expenditure, on foraging trips kittiwakes expended between 19.5 ± 1.4 and 48.2 ± 2.2 kJ h^{-1}, averaging 38.2 ± 1.9 kJ h^{-1}. Of all 153 foraging trips measured, 62% of them cost less than 100 kJ of energy, with 84% costing less than 200 kJ. Shorter foraging trips were highly variable in time spent flying, but had the highest recorded percentage of time spent flying across foraging trips (Fig. 4). Overall, proportion of time spent in flight decreased significantly with duration ($t_{124} = -5.52$, $P < 0.001$). As foraging trips which lasted longer tended to have a lower proportion of time spent in flight, the hourly rate of energy expenditure for such trips was lower than for shorter trips. No kittiwakes exhibited extremely high percentages of time spent in flight during foraging trips of longer duration, with the maximum estimated energy expenditure of 368 ± 19 kJ corresponding to a trip lasting 10.29 h, of which 57.6% (5.92 h) was spent flying.

Foraging trip duration alone was a poor predictor of estimated foraging expenditure. Although the R^2 value of the linear fit between foraging trip duration and total energy expenditure (Fig. 5a) was high at 0.88, estimated energy expenditure differed from that predicted by this relationship by an average of 19.8%, ranging from 0.1 to 60.1% (Fig. 5b). This translates to a mean difference in energy expenditure of 20.1 kJ (range 0.1–95.7) over the foraging trip.

Discussion

Activity and energy expenditure over 24 h

Across the 24-h day, individual kittiwakes spent the majority of time exhibiting the less energetically expensive behaviours of either attending their nest or being on the water. A greater percentage of time allocated to less energetically expensive behaviours could be due to intrinsic or extrinsic limiting factors (Humphreys, Wanless & Bryant, 2006; Welcker *et al.*, 2009, 2010). For time spent flying to be limited intrinsically would suggest that there is a physiological reason preventing

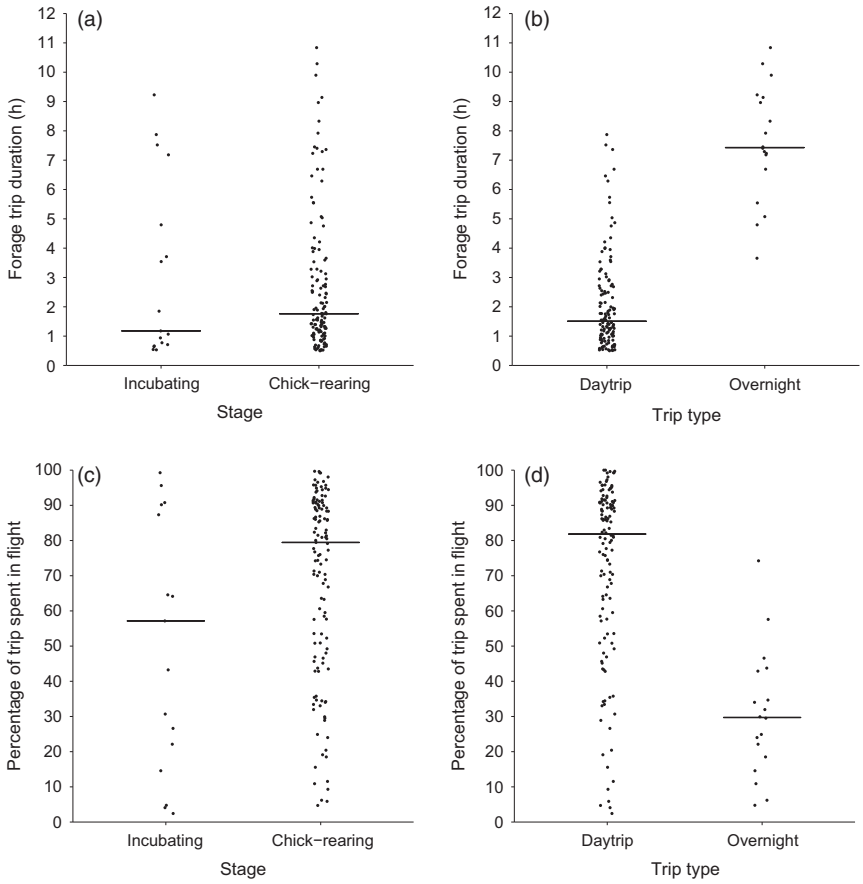

Figure 2 Duration of foraging trip dependent on breeding stage (a) and trip type (b), and proportion of individual foraging trips spent flying dependent on breeding stage (c) and trip type (d). Black dots indicate individual foraging trips, black lines indicate the median value.

kittiwakes from flying for more of the day, whereas extrinsic limiting factors would suggest that their behaviour was determined by an external feature such as prey availability. Both intrinsic and extrinsic factors could, and are likely to be, influencing the patterns in behaviours we recorded (Humphreys *et al.*, 2006). To elucidate the causes of the potential limitations to daily activity presented, it would be ideal to combine measurements of time spent flying with indicators of rates of prey acquisition and measures of body condition. This has been achieved in two studies on chick-rearing murres, which found both an energetic ceiling determined by the ability of individuals to digest food (Elliott *et al.*, 2014b), and behavioural compensation limiting DEE (Elliott *et al.*, 2014a).

It is clear from our results that chick-rearing birds spend a greater proportion of time flying than do incubating birds (Fig. 1). This increased amount of time spent flying is likely to be a result of adults needing to make regular foraging trips to provision chicks (Rishworth & Pistorius, 2015). In contrast, during incubation, foraging trips are less frequent due to the need for adult kittiwakes only to meet their own energy requirements (Ponchon *et al.*, 2014). With flight being energetically expensive (Jodice *et al.*, 2003), it stands to reason that incubating birds are more capable than chick-rearing birds of mediating their energy expenditure by flying less. Indeed, an increase in time spent flying is likely to be the most important factor in the greater DEE recorded during chick-rearing in comparison to incubation identified in many bird species (e.g. Humphreys *et al.*, 2006; Rishworth, Tremblay & Green, 2014). For kittiwakes, such an increase in energetic expenditure during this period is a likely contributor towards them having a poorer body condition, greater levels of stress and a greater likelihood of breeding failure while chick-rearing than when incubating their eggs (Kitaysky, Wingfield & Piatt, 1999; Ponchon *et al.*, 2014). It should be noted, however, that the sample size for incubating birds in this study was much lower than that for chick-rearing birds, thus for incubating birds, the time and energy estimates must be considered with caution.

Activity and energy expenditure over foraging trips

By examining the time-activity and time-energy budgets at the level of the foraging trip, we have provided a more detailed level of behavioural information than has been previously available for kittiwakes. We have highlighted a large degree of variation in the relationship between trip duration and

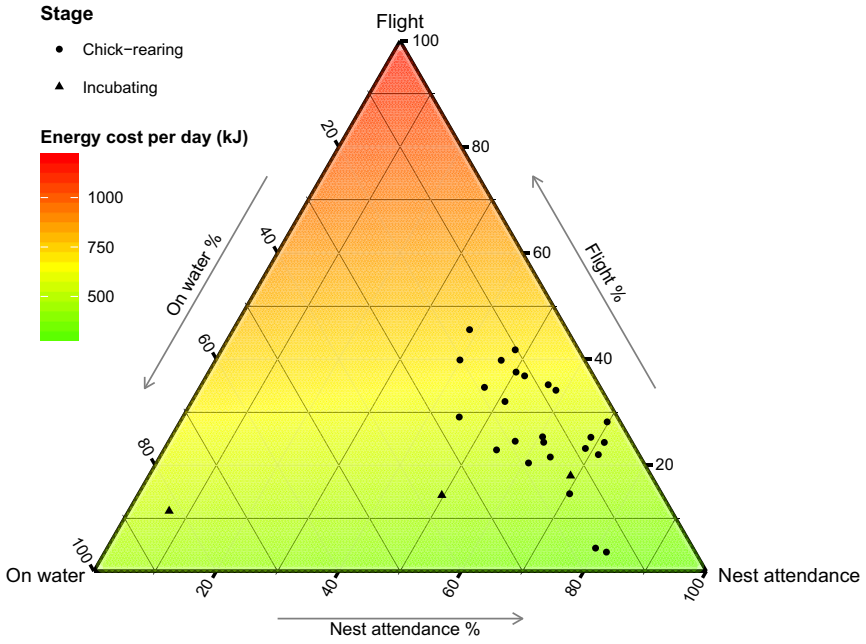

Figure 3 The daily energy expenditures of kittiwakes of average mass, dependent on allocation of time to nest attendance, being on the water, and flying. Each black symbol represents a full 24-h period of recorded activity from an individual incubating (triangle) or chick-rearing (circle) kittiwake. Percentage of time spent in each activity should be read parallel to the direction of the tick marks for each axis respectively.

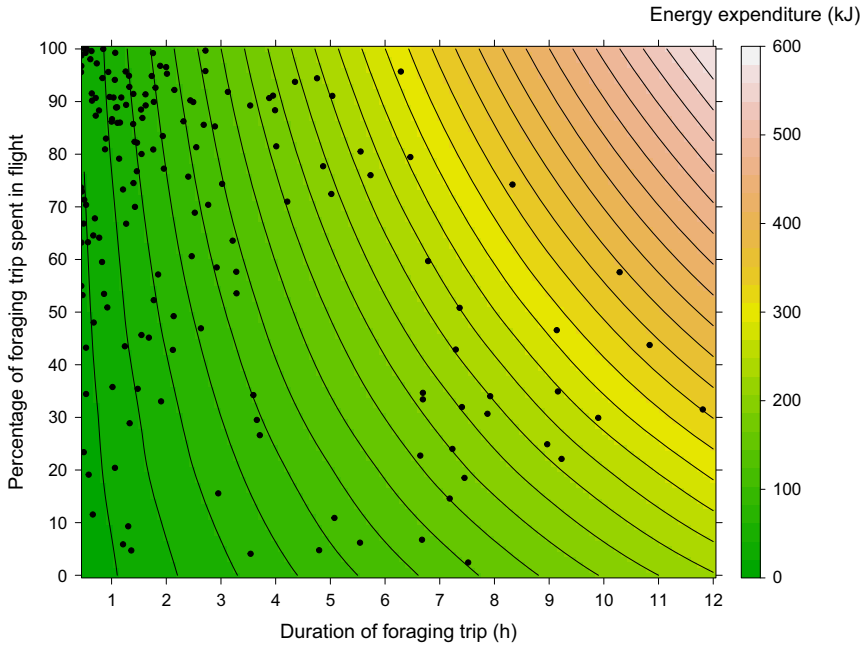

Figure 4 Total energy cost (kJ) of foraging trips dependent on percentage of trip spent flying in relation to duration of foraging trip. Black dots indicate values from individual foraging trips from 21 kittiwakes.

proportion of time spent flying. Although foraging trip duration correlated positively with total energy expenditure (Fig. 5), the variation around a positive linear relationship between trip duration and energy expenditure had an average error of 19% when compared to estimates of energy expenditure which took proportion of trip spent flying into account (Fig. 5). Notably, when looking at the proportion of time spent flying plotted against duration of foraging trip (Fig. 4), there is an absence

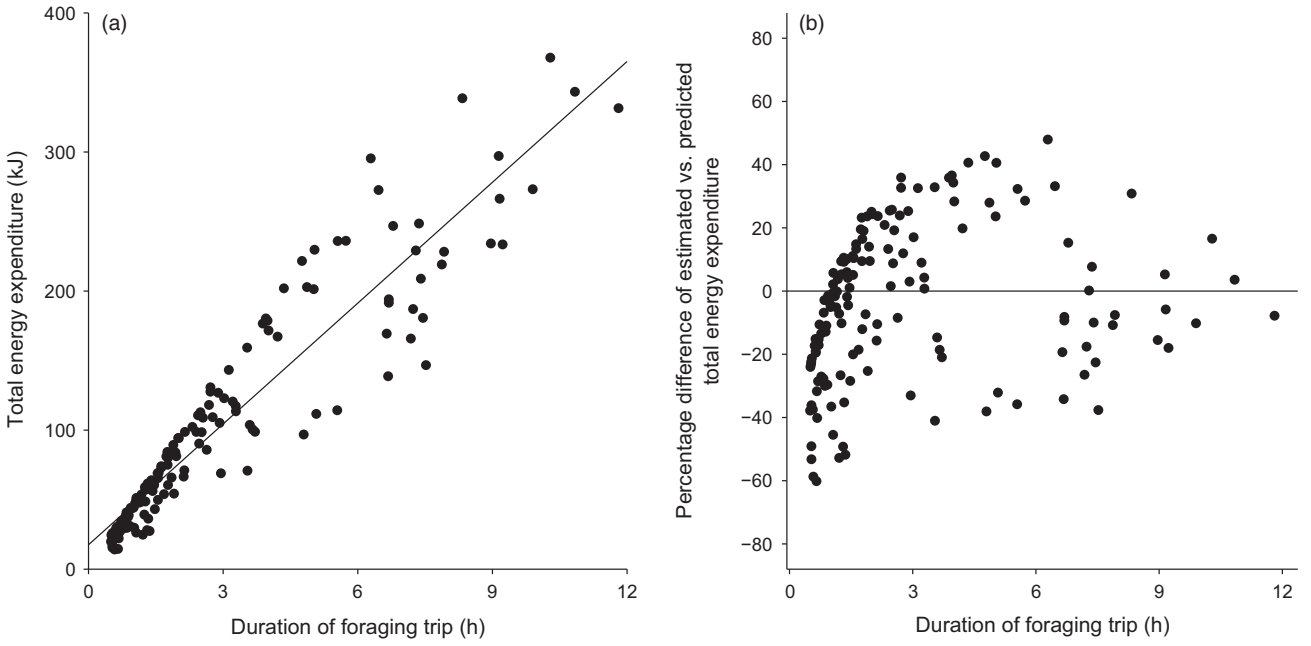

Figure 5 (a) The relationship between foraging trip duration and total estimated energy expended during each foraging trip. The least squares regression line of best linear fit is shown. (b) Difference in total measured energy expenditure as a percentage of total energy expenditure predicted from foraging trip duration using the linear relationship displayed in (a).

Table 1 Estimates of mean ± SD daily energy expenditure and mean body mass of chick-rearing kittiwake adults from studies published to date

Study	Energy expenditure (kJ d^{-1})	Mass (g)	Location
Current study	559 ± 19	365	Puffin Island, UK
Jodice *et al.* (2002)	724 ± 171	368	Middleton Island, Alaska
Golet *et al.* (2000)	786 ± 73	404	Shoup Bay, Alaska
Thomson *et al.* (1998)	863 ± 177	386	Hornoya, Norway
Welcker *et al.* (2010)	882 ± 88	386	Kongsfjorden, Norway
Jodice *et al.* (2003)	934 ± 301	NA	Valdez, Alaska
Schultner *et al.* (2010)	960 ± 118	377	Kongsfjorden, Svalbard
Gabrielsen *et al.* (1987)	992 ± 273	390	Hopen Island, Svalbard
Welcker *et al.* (2014)	998 ± 272	392	Middleton Island, Alaska

All previous studies used the DLW method for estimating energy expenditure.

of data points in the top right hand corner where energy costs are highest. This provides some evidence towards the presence of behavioural compensation, whereby individuals limit total energy expenditure on longer trips by spending a lower proportion of time flying. This could also be seen as providing support for the idea of an energetic ceiling, whereby individuals are constrained in their total energy expenditure at this scale (Welcker *et al.*, 2010; Elliott *et al.*, 2014b). This finding also highlights the inadequacy of using foraging trip duration alone as a proxy for energy expenditure. Foraging trip duration is often used as a direct indication of energy expended when away from the nest (Welcker *et al.*, 2010; Rishworth *et al.*, 2014), as well as an indication of foraging conditions and food availability (Kitaysky *et al.*, 1999). However, we suggest that both trip duration and time spent flying should be considered together before making inferences relating to energy expenditure. Indeed, to further improve estimates of energy expenditure when away from the colony, wind conditions and time spent in either flapping or gliding flight could be taken into account.

Estimates of energy expenditure

The absolute DEE values we estimated for breeding kittiwakes are lower than existing published studies (Table 1). Reports of energy expenditure differ between kittiwake colonies (Table 1) and as such it may be that kittiwakes on Puffin Island are less active and expend less energy than those from other colonies. There are many possible explanations for this. For example, low intraspecific competition due to low breeding density of kittiwakes on Puffin Island could have reduced the amount of energy they needed to expend to successfully forage (Ballance *et al.*, 2009), relatively short day lengths at Puffin Island compared to higher latitude colonies could limit time spent foraging, and/or the presence of the accelerometer itself may have decreased the amount of time kittiwakes spent flying (Chivers, Hatch & Elliott, 2016).

Methodological considerations may also explain our comparatively low estimates of energy expenditure. The flight model we used to estimate flight costs has been shown to sometimes misestimate energy expenditure in comparison to empirical estimates (Mcwilliams *et al.*, 2004; Schmidt-Wellenburg *et al.*, 2007). The only other study providing activity-specific estimates of energy expenditure for kittiwakes, Jodice *et al.* (2003), suggests that flight is 5.6 times more expensive than nest attendance, whereas our approach estimates it to be 3.5 times more expensive. By following Jodice *et al.* (2003) and multiplying basal metabolic rate by activity-specific factors, our estimates of DEE increase to 833 ± 23 kJ d^{-1} (detailed in Appendix S1). Although the suitability of multiplying basal metabolic rates to estimate energy expenditure during activity is contested (Pennycuick, 2008), this does indicate that low flight costs are likely driving our low energy expenditure estimates. Furthermore, the estimates of DEE we have presented have a strong linear correlation ($r^2 = 0.97$, Appendix S1) with those we achieved by following the method in Jodice *et al.* (2003). This indicates that between these methods, it is only the absolute values of energy expenditure that differ, rather than the key biological findings.

Our approach also does not take into account variation in energy expenditure relating to varying degrees of movement during behaviours. Energetic variation during behaviours may arise from sources such as switching between flapping and gliding flight, or from take-offs and landings (Shaffer *et al.* 2001). Amount of body movement can be quantified from acceleration data as dynamic body acceleration (DBA). DBA can be calibrated with energy expenditure either through oxygen consumption measurements in the laboratory (Halsey *et al.*, 2009a) or with estimates from the DLW technique (Elliott *et al.*, 2013). This has been attempted for kittiwakes by Kristiansen (2014), who regressed DBA against energy expenditure as measured through the DLW technique for five birds, having discarded measurements from a sixth bird due to it being a heavy outlier. By applying the equation from their linear regression to calculations of DBA from our study birds, we estimate DEE to be 1130 ± 28 kJ d^{-1} (Appendix S1). Estimates of individual DEE we achieve by following this approach have a positive linear relationship with an r^2 value of 0.70 when correlated with the estimates we have presented (Appendix S1). This indicates that the overall trends found using these two methods do correspond, however, at the individual level, estimates of energy expenditure are variable depending on the method used. There are some serious limitations with this approach however. Firstly, a number of previous studies using DLW on seabirds have shown that estimate errors on an individual basis tend to be very large (Shaffer, 2011) and as such they should not be relied upon (Butler *et al.*, 2004), and in addition to this, the small sample size of the study severely limits the confidence we can have in the reported linear relationship. Furthermore, the relationship between rate of energy expenditure and DBA is not always constant across different behaviours and as such different equations for different behaviours are required to accurately estimate metabolic rate (Green *et al.*, 2009; Elliott *et al.*, 2013).

Estimates of energy expenditure from this study, Jodice *et al.* (2003) and Kristiansen (2014) vary substantially in absolute estimates of energy expenditure, although they do all positively correlate (Appendix S1), thus indicating that our overall biological findings, if not the exact estimates of energy expenditure we produce, are robust regardless of method used. To identify if our low DEE estimates are due to biological or methodological reasons, detailed time-activity information is required from other colonies. The method we employ is essentially an update of traditional observation-based time-activity budgets; it is simple to implement and allows insights into variations in behaviour and their energetic consequences at a range of temporal scales and without the need for logistically demanding proxy calibrations.

Conclusion

By constructing time-activity and time-energy budgets through coupling accelerometry data with activity-specific rates of energy expenditure, we have highlighted key features of the behavioural ecology of kittiwakes as well as the deficiency of examining forage trip duration alone when considering energy expenditure in breeding seabirds. In particular, we have provided further evidence for behavioural compensation linked to a limitation in the amount of energy individuals expend. A lack of studies using a similar method to ours has not allowed us to make a detailed comparison of DEE to that of kittiwakes at other colonies; however, the relative simplicity of our approach should prompt others to employ it.

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Supporting Information

Additional Supporting Information may be found in the online version of this article:

Appendix S1. Comparison of estimates of energy expenditure estimated from three different methods.

Table S1. Estimates of energy expenditure for each study bird based on the method presented in this study as well as from Jodice *et al.* (2003) and Kristiansen (2014). Each row represents an individual bird on 1 day, hence repetitions under Bird ID.

Figure S1. Daily energy expenditure as estimated from this study, which applies activity-specific estimates of energy expenditure to time-activity budgets, Jodice *et al.* (2003), which estimates energy expenditure using activity-specific multiplications of BMR, and Kristiansen (2014), which estimates energy expenditure based on a linear regression between ODBA and energy expenditure measured via the DLW technique.

Figure S2. Mass-specific estimates of energy expenditure as estimated by dividing the estimates used in Fig. 1 by individual kittiwake mass (g).

Figure S3. Correlations between daily energy expenditure from the three methods detailed in Fig. 1. All values are in kJ d^{-1}.